# COMPARISON OF JUNIPER POPULATIONS ON AN OZARK GLADE AND OLD FIELDS

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## INTRODUCTION

Using comparative morphology as criteria, I presented evidence in an earlier paper (Hall, 1952) that *Juniperus virginiana* L. has differentiated into five geographic races, and two of these races, called Typica and Ozark, were described in detail. Typica is known to the horticulturist as the Eastern form and may be characterized as the very tall, narrowly pyramidal tree found from Virginia to southern Illinois. Within its present distribution Typica is concordantly variable, and at least so homogeneous that it seems to be carrying no introgressant genes from other species. The influence of Typica in the juniper populations of the Ozark Plateau is not evident even though isolated plantings of this race are to be found on the western banks of the Mississippi River from St. Louis southward, usually about old farmsteads. The only other race of red cedar which occurs occasionally in the St. Louis area is the Northern, which is characterized by high frequencies of the spire-like form known as var. *crebra,* by crooked fruiting peduncles, and a preference for well-drained, sandy soils with a slightly acid reaction. I postulated that this Northern race may be the consequence of a few genes from *J. horizontalis* becoming stabilized in red cedar. The Northern race, with its tendency toward suppressed lateral branching, follows the glacial drift down the Mississippi River, and where the periglacial loess occurs these junipers are abundant. South of the loess deposits, particularly in the vicinity of St. Louis, juniper populations closely resembling the Northern race occur sporadically.

The Ozark race is indeed the most abundant and important in the St. Louis area and represents red cedar throughout the Southwest. The Ozark race, which is the result of introgression by genes of *J. Ashei* Buchholz into *J. virginiana* L., includes a highly variable assemblage of junipers distributed from central Texas across eastern Oklahoma and the Boston Mountains of Arkansas through the Missouri Ozarks to the Mississippi and Missouri rivers. Introgression by genes of *J. Ashei* into red cedar has probably occurred repeatedly, at least during the Pleistocene, and current mixing is evident in restricted areas where extensive hybrid swarms exist.

The purpose of this investigation was to determine the differences between the habitats in relation to the differences in the variability within and between populations of these Northern and Ozark races of junipers. The habitats studied are close together, less than a mile apart, and are surrounded by many hundreds of populations of junipers both large and small. It was thought that these habitats may select from this large gene pool adaptive genotypes which may vary from population to population proportionately to the habitat differences.

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In the spring of 1952 I was granted a leave from the Cranbrook Institute of Science to be a guest lecturer in Genetics and Evolution at the Henry Shaw School of Botany, Washington University, St. Louis, Missouri, and to take over Dr. Edgar Anderson's class during his absence. This study was part of a project undertaken by Dr. Anderson's class under my direction.

I am most grateful to Dean Henry N. Andrews for his advice and cooperation and to Dr. Anderson for his enthusiasm in regard to field studies as well as his helpful criticism. The study was carried out in the native tracts of the Missouri Botanical Garden Arboretum, Gray Summit, Missouri, which is approximately forty miles southwest of St. Louis on US Highway 66. I am especially grateful to Mr. August P. Beilmann, Superintendent of the Arboretum, for his cooperation and detailed knowledge of land use in the Ozark region.

## GENERAL DESCRIPTION OF THE AREAS

The areas studied are within the Missouri Botanical Garden Arboretum, which is situated 40 miles southwest of St. Louis, Missouri, just south of the junction of Highway 66 and Highway 50 near Gray Summit, a hilly region principally of weathered dolomitic limestones in the northern portion of the Ozark highland. The climate is designated by Thornthwaite as $BB^1r$ (humid, mesothermal, with precipitation adequate at all seasons). Records in St. Louis for the past hundred years show such variations in precipitation that no general trends are evident, so that it is difficult to judge whether climatic amelioration or deterioration is in process. The Ozark Plateau is a part of the Oak-Hickory Forest Region described by E. Lucy Braun (1950) as the Interior Highlands, Southern Division, which lies essentially south of the glacial border. Braun wrote:

> "The Southern Division is characterized by the prominence of southern species of oaks and hickories, as *Quercus stellata, Q. marilandica, Q. Shumardii* (and var. *Schneckii*), and *Carya Buckleyi* (var. *arkansana* and var. *villosa*), and in the bottomlands, *Q. nigra, Q. lyrata, Carya Pecan, C. myristicaeformis,* and *C. aquatica* . . . . Prairie openings, limestone glades, and balds locally interrupt the forest cover."

Those who know the Ozark landscape consider these local interruptions of forest cover as the particular mark of beauty of the uplands, and the "openness" was a major feature in selection for settlement in pioneer days. Visitors to the Ozarks from foreign countries usually are most impressed by the red cedar glades which are island playgrounds in the present-day dense oak woods. In the proper season these open areas serve as edge for much wildlife activity, and perhaps the most characteristic features in this wise are the summer call of the chuck-will's-widow and the "booming" of the nighthawk that so often chooses a glade for his target.

The soils indicate a long history of open conditions where prairie vegetation, probably maintained by fire and grazing, played a very important role in the development of soil horizons. Soils in the area are characteristic of prairie-forest transition regions and are much like the nut-structured prairie-forest Grood soils of continental sub-humid steppes, being intermediate between chernozems and podsols. Regardless of its history of prairie development, the Ozark region has a forest climate and probably has had since the end of the xerothermic period. Thus the climax plant formation, which is of course subject to continual change, may be the oak-hickory forest which has been spreading extensively throughout Missouri roughly in the last hundred years. Beilmann and Brenner (1951) and Etter (1953) report this trend in their studies of Ozark vegetation. It is not likely that any region has ever had a vegetational mantle entirely in equilibrium with climate alone, for other factors affecting balance are legion—e. g. nature of geological substrate, grazing and browsing, fire, and man. Rather, as Sauer (1950) has pointed out, "Plant associations are contemporary expressions of historical events and processes, involving changes in environment and biota over a large span of geologic time." However, Braun (1950) stated that knowledge of these historical events and processes is very scant even though general trends seem to be quite clear.

The history of land usage in the Gray Summit area is not known in detail, but titles to land were granted beginning about 1850, nearly 50 years after the first settlers, mostly French, began to locate along the major waterways in what is now Franklin County, and over 80 years after St. Louis was founded, also by the French. Evidence of timber cutting, heavy grazing and burning variously from the time of settlement until the Missouri Botanical Garden acquired the property in 1925 is clear and common. Apparently, in the days before the settlement of the region most of the timber was found on the headwaters of the creeks and was scattered, giving a prairie- or park-like aspect presumably as a result of a somewhat drier climate than today and the effects of grazing, fire, etc. The timber, where dense enough to be called woodland, was usually situated in the rough lands or dissected headwaters of the streams where it was largely safe from fire.

Today the Ozarks are well covered with close forests, and the once open areas show signs of rapid forest encroachment; old fields develop rapidly to forest, but the glades show little invasion by woody species even when protected from fire or grazing. Steyermark (1940) made a vegetational survey of Missouri which covered fifteen years of extensive observation, and even though the survey was strictly qualitative it was detailed enough to permit rough comparisons with present-day conditions. He stressed the role of rock strata and soil, i. e., edaphic factors, in determining the distribution of plant associations. He described six plant associations and many more associes based on differences in soil, slope, and water availability; in his conclusions he favors the polyclimax concept subscribed to by Domin, Gams, Gleason, Tansley, and Du Rietz. He indicated that the glade flora was the result of edaphic factors, and in most sites would eventually support a maple-white oak association which in the Ozarks seems to be restricted to slopes and bluffs with neutral to alkaline soils underlain by limestone.

*The Glade.*—The Glade, which is one of several within the boundaries of the Missouri Botanical Garden Arboretum, may be characterized as a small open space (open glade), approximately 60,000 square feet in extent, covered by grasses and junipers surrounded by a closed area (closed glade), or buffer, approximately fifty feet in width, chiefly composed of junipers and chinquapin oaks and situated on a west-facing slope (upward ENE, 10°20′). The area studied constituted a rectangle 400 × 150 feet, approximately the total extent of the open glade. In this study the term Glade refers to the open glade within the enclosure studied.

This same glade was described by Erickson, Brenner, and Wraight (1942), who demonstrated a direct correlation between the structure and composition of the glade flora and the occurrence of a dolomite stratum at or near the surface. The glade soil is very shallow (averaging about 4 inches), organically rich and derived from a dolomitic rock which under the open glade is a thin, porous dolomite locally known as "cotton-rock," an upper stratum of the Cotter Formation, and lies unconformably on the Jefferson City Formation, both in the Canadian Series of the lower Ordovician. Under the closed glade a less porous dolomite with lower magnesium content is covered by a fairly thin mantle of Union Silt Loam. The dense oak-hickory upland forest on the Union Silt Loam gives way to red cedar-chinquapin oak forest at the periphery of the glade, but wherever the "cotton-rock" occurs it drains the area sufficiently that the red cedar-chinquapin oak forest is fairly well stabilized. In winter and spring, as a consequence of greater precipitation and less evaporation, the open glade ("cotton-rock" stratum) is wet, often with standing water, while in summer and fall, when precipitation effectiveness is least, the porosity of the rock permits rapid drainage which results in rather extreme dryness in the upper few feet of the stratum. I have been frequently observing several of these glades since 1947, and, besides the rather obvious seasonal cycle of wetness and dryness, there are fluctuations every few years which markedly affect the population density of the species and the cover. In order for the perennials, in particular, to be successful in the glade community, they must be able to withstand fairly great fluctuations of the environmental conditions.

*The Old Field.*—The Old Field is situated on a gently sloping knoll below the orchid greenhouse. The upward slope (5°10′) is NNW facing SSE. The knoll is covered by Union Silt Loam and probably will eventually support an oak-hickory forest. On this knoll a plot 60,000 square feet in extent was laid out as a rectangle 300 × 200 feet.

Prior to 1925 the area was under cultivation in the traditional "Ozark fashion." A few acres of beans, peas, and corn were planted, rows running uphill, and tilled by means of the mouldboard plow and mule driven by a tenant farmer. In 1925, when the property was acquired by the Arboretum, this field was badly eroded and almost bare of vegetation, but since 1925 it has not been grazed or burned, and the revegetation has been accomplished in the last 28 years.

At present, the arborescent growth on the Old Field consists of scattered junipers, black oak, white ash, and thickets of red elm. Wisteria is an abundant shrub, having invaded the field from plantings nearby. The upper edge of the sloping field supports a growth of sugar maple, white ash, black oak, shingle oak, post oak, black cherry, smooth sumac, buckbrush, and poison ivy. The middle portion of the field consists of thickets or clumps of red elm saplings with a maximum height of about ten feet, and a thick growth of smooth sumac and wisteria. On the lower slope which drains into a tiny creek are growing black oak, white ash, northern red oak, persimmon, rough-leaved dogwood, winged sumac, poison ivy, woodbine, and summer grape.

The oldest arborescent growth is made up of persimmon, post oak, black oak, and shingle oak, which apparently invaded the field approximately five years after its abandonment. Then northern red oak, sugar maple, white ash and red cedar came in six to eight years after abandonment. At any rate, the older specimens of red cedar were twenty years old, eight years having elapsed since abandonment of the field. The rate of invasion by red cedar depends on the balance of several variables such as the number and proximity of seed-producing plants, condition of the invaded area, amount of cover, slope, pH, etc. Drew (1942), in his studies of abandoned crop-land in the Cedar Creek area, Boone and Callaway counties, Missouri, found that five years after abandonment sassafras, persimmon, shagbark hickory, post oak, and shingle oak invaded; after six to seven years, American elm; after eight to ten, northern red oak, sugar maple, white ash, honey locust, and black walnut; after eleven to twelve years, red cedar and black oak.

In the herb layer the general cover consisted of fairly evenly distributed clumps of broom-sedge with Kentucky blue-grass in swales and level places bordered by clumps of little blue-stem. On the up-slope, broom-sedge, tall red-top, Canada goldenrod, and old field goldenrod were conspicuous. From midway to the bottom of the slope were these same species plus dewberry *(Rubus flagellaris)* and *Aster pilosus*. Here and there were almost bare sandy slopes, a few feet in extent, consisting of stands of triple awn-grass with a few lichens and mosses. Directly beneath the crowns of most of the larger trees were areas covered by lichens and mosses.

*Cedar Hill.*—Another old field, here called Cedar Hill, is an exclosure with a gentle slope from west to east mowed annually with a sickle-bar and covered with well-spaced red cedar, black oak, black cherry, honey locust, and red elm. The shrub layer consists of dewberry *(Rubus flagellaris)*, smooth sumac, trumpet-vine, buckthorn, aromatic sumac, large clumps of buckbrush, partridge pea, and seedlings of sassafras, shingle oak, and persimmon. The herb layer consists principally of Canada blue-grass, triple awn-grass, tall red-top, *Panicum capillare*, and frequent clumps of broom-sedge, scattered clumps of little blue-stem, and occasional clumps of mountain mint and ironweed. Dewberry *(Rubus flagellaris)* was scattered fairly evenly throughout the field.

The junipers average about 30 feet in height and thirty years of age, somewhat younger than those of the Glade. The juniper reproduction in the exclosure was negligible. Although there were abundant seedlings, particularly at the edge of the crowns of those mature junipers bearing berry-cones, all were below sickle-bar height and usually under three years of age. Just outside the exclosure and in the general area juniper reproduction was very good, and ages up to thirty-five years were represented. Species composition was not analyzed because of the artificial situation. In the meadow the juniper population in an area of 60,000 square feet was sampled. In general features this meadow is closely similar to the Old Field. The soil is Union Silt Loam but much deeper since Cedar Hill lies above an old river channel. The Cedar Hill population was included in this study because of its intermediate position morphologically between the Glade junipers and those of the Old Field.

## METHODS OF STUDY

Several factors were studied for the Glade and Old Field in order to make comparisons. Species composition, distribution of juniper seedlings, and the population structure of junipers were studied, and the data appear in Tables I–II, figs. 1–3, and pls. 20–21. Frequency was used as a quick method of measuring species composition. The Glade and the Old Field were divided into four plots by staking out the diagonals. Along the diagonals alternating from one side to the other, 20 quadrats (1 meter in size) were laid out, equally spaced from the center. Preliminary work was done in late spring of 1952, but other surveys were made in late spring and late summer of 1953. The presence of species in each quadrat was tabulated and the results for the Glade and Old Field appear in Table I. The areas studied seemed sufficiently homogeneous for the use of 1-meter quadrat size, specifically to determine the species composition of the herb layer. A sample area about 0.5 per cent of the total was used. A compromise in favor of a small sample area was made because of the limited time the class could be in the field.

Variations of the juniper populations were measured by pictorialized scatter diagrams as demonstrated in *Juniperus* in a previous paper (Hall, 1952). Five characters were scored: gland length-width ratio; length of whip (longshoot) leaf; length of terminal whip; length of lateral whip; on secondary shoots, the per cent of tertiary branches which have the decussate leaf arrangement. Two of these characters were also analyzed by use of the parameters of the log-normal curve which the data fit. These data, when plotted on logarithmic probability paper, result in a straight line.

In an attempt to get some estimate of seed-dispersal pattern, the distribution of seedlings was studied. Observations were made to determine the role that birds, mammals, and gravity may play in seed dispersal.

## SPECIES COMPOSITION

Rough comparisons were made of species composition of vascular plants for the Glade and the Old Field. Only one quadrat size was used and no attempt was made to obtain quantitative data on density or cover. For convenience a frequence index after the method of Raunkiaer (1918) was made up for the Glade and the

Old Field. The percentage of frequence for a given species is the percentage ratio the plots on which the species occur bear to the whole number of plots sampled. Raunkiaer found that the greatest number of species had the least frequence; and that as the frequence increased the number declined steadily, until at the highest frequence the number increased slightly. Raunkiaer used five frequence groups, A, B, C, D, and E, designating the species of frequence 1–20 per cent, 21–40 per cent, 41–60 per cent, 61–80 per cent, 81–100 per cent, respectively. His law of distribution, determined from quadrat studies in Europe was $A > B > C \overset{\geq}{\underset{<}{=}} D < E$; the actual percentages were approximately 53, 14, 9, 8, 16. In eastern America, Kenoyer (1927), found that 69, 12, 6, 4, 9 per cent were more characteristic.

In this study the Glade had a frequence index of 28, 8, 2, 2, 2 or $A > B > C = D = E$. This index is similar to that found by Kenoyer in his studies for America and indicates a fairly high proportion of sporadic species and a very few acting in a "dominant" role. The Glade has uniformly distributed patches of *Sporobolus neglectus,* and the size of each patch fluctuates somewhat from year to year. When the patches are smaller, more *Bouteloua curtipendula* and forbs are in evidence. In good years the Glade has a good cover contributed principally by a very small number of species even though there is an appreciable number of sporadic species between the clumps of the cover plants.

The Old Field index was 22, 3, 8, 5, 0 or $A>B<C>D>E$. This somewhat irregular result is a product of the heterogeneous nature of the Old Field flora. There are a large number of sporadic species, a fairly large number of species intermediate in frequence, and no "dominants." The floral composition and vegetational structure are markedly different from those of the Glade. Factors of competition and selection are less delicately balanced in the Old Field, and these factors undoubtedly cause the population structure of the junipers there to be different from that of the Glade.

Table I lists the species and their frequencies found in sampling 0.5 per cent of the area studied. Only the under-story is represented. Woody plants in the list were seedlings or sprouts in size class 1 (0–0.9 feet) of Weaver and Clements (1938). The Old Field had seven species of woody plants represented in this size class for the area surveyed, which compares with nine species of similar size found by Drew (1942) to be common in old fields twenty-five years after abandonment. In the Old Field all sizes of woody plants were abundant up to size class 4 (3.6–9.5 inches D.B.H.), but on the Glade very few specimens larger than size class 1 were seen, suggesting a high seedling mortality. The frequency data in Table I show that the Glade and Old Field are quite different in species composition and suggest a difference in the pattern of succession. The Glade is a "prairie" association with *Andropogon scoparius* and *Rudbeckia missouriensis* contributing most to its aspect and with *Andropogon scoparius* and *Sporobolus neglectus* contributing most to the cover. Even though there is some fluctuation in abundance from year to year. there are definite dominants, a good variety to the flora, and a stability in its overall composition which suggests that succession is very slow and that the Glade

TABLE I

SPECIES LIST WITH FREQUENCIES FOR UNDER STORY OF GLADE AND OLD FIELD*

| Glade | Frequencies | Old Field |
|---|---|---|
| 1. *Sporobolus neglectus* | 1.00 | ——— |
| 2. *Carex Crawei* | .90 | ——— |
| 3. *Andropogon scoparius* | .80 | *Poa pratensis* |
| 4. *Houstonia longifolia* | .75 | *Rubus flagellaris* |
| 5. ——— | .70 | *Andropogon virginicus* |
| 6. ——— | .70 | *Aster pilosus* |
| 7. ——— | .65 | *Desmodium glabellum* |
| 8. *Euphorbia corollata* | .60 | ——— |
| 9. *Rudbeckia missouriensis* | .55 | *Rumex hastatulus* |
| 10. ——— | .55 | *Oxalis stricta* |
| 11. ——— | .50 | *Panicum virgatum* |
| 12. ——— | .50 | Lichens |
| 13. *Sisyrinchium campestre* | .45 | *Erigeron strigosus* |
| 14. ——— | .45 | *Taraxacum officinale* |
| 15. ——— | .45 | *Hieracium Gronovii* |
| 16. ——— | .45 | *Campsis radicans* |
| 17. *Hypericum prolificum* | .40 | *Triodia flava* |
| 18. *Gaillardia pulchella* | .40 | ——— |
| 19. *Echinacea pallida* | .40 | ——— |
| 20. *Ruellia humilis* | .35 | ——— |
| 21. *Oenothera missouriensis* | .35 | ——— |
| 22. *Heliotropium tenellum* | .35 | ——— |
| 23. ——— | .30 | *Achillea millefolium* |
| 24. *Viola pedata* | .25 | *Parthenocissus quinquefolia* |
| 25. *Selaginella rupestris* | .25 | Mosses |
| 26. *Juniperus virginiana* | .25 | ——— |
| 27. *Viola papilionacea* | .20 | *Ulmus rubra* |
| 28. ——— | .20 | *Celtis occidentalis* var. *pumila* |
| 29. *Coreopsis lanceolata* var. *villosa* | .15 | *Hypericum punctatum* |
| 30. *Ulmus rubra* | .15 | *Prunus serotina* |
| 31. ——— | .15 | *Cercis canadensis* |
| 32. ——— | .15 | *Rhus aromatica* |
| 33. Mosses | .10 | *Juniperus virginiana* |
| 34. *Eleocharis compressa* | .10 | *Asplenium platyneuron* |
| 35. *Aster oblongifolius* | .10 | *Ambrosia artemisifolia* |
| 36. *Zizea aurea* | .10 | *Allium vineale* |
| 37. *Monarda citriodora* | .10 | *Solanum carolinense* |
| 38. *Cercis canadensis* | .10 | *Carex Haydenii* |
| 39. *Rhamnus caroliniana* var. *mollis* | .10 | *Eragrostis spectabilis* var. *sparsihirsuta* |
| 40. *Comandra Richardsiana* | .10 | ——— |
| 41. *Lotus americanus* | .10 | ——— |
| 42. *Orobanche uniflora* | .10 | ——— |
| 43. *Acalypha graciliens* | .10 | ——— |
| 44. *Panicum virgatum* | .10 | ——— |
| 45. *Triodia flava* | .05 | *Veronica arvensis* |
| 46. Lichens | .05 | *Asclepias syriaca* |
| 47. *Bumelia lanuginosa* var. *oblongifolia* | .05 | *Acer saccharum* |
| 48. *Fraxinus americana* | .05 | *Physalis pruinosa* |
| 49. *Monarda Russeliana* | .05 | *Pentstemon pallidus* |
| 50. *Acer saccharum* | .05 | *Sporobolus neglectus* |
| 51. *Anemonella thalictroides* | .05 | *Daucus pusillus* |
| 52. *Bouteloua curtipendula* | .05 | *Antennaria fallax* |
| 53. *Silphium laciniatum* | .05 | *Potentilla recta* |
| 54. *Psoralea esculenta* | .05 | *Galium aparine* |
| 55. *Quercus Muehlenbergii* | .05 | *Poa compressa* |

| Glade | Frequencies | Old Field |
|---|---|---|
| 56. *Pellaea atropurpurea* | .05 | *Rhus Toxicodendron* |
| 57. *Fimbristylis Drummondii* | .05 | ———— |
| 58. *Petalostemum purpureum* | .05 | ———— |
| 59. *Symphoricarpos orbiculatus* | .05 | ———— |
| 60. *Pentstemon pallidus* | .05 | ———— |

* Nomenclature after Gray's Manual of Botany, 8th edition, 1950.

community is one of real integrity. Because of the uniformity in distribution of *Andropogon, Sporobolus,* and *Bouteloua* the quality of the cover on the Glade can be determined fairly well with frequency data. In a good year the clumps of *Andropogon* are larger, denser, and more frequent. The *Sporobolus* effectively fills in between the clumps. In a dry or unseasonable year the *Andropogon* may lose ground, the *Sporobolus* to a lesser extent, but the *Bouteloua* may increase considerably. Thus, one can tell when the Glade is in good condition, so far as climatic fluctuations are concerned, by the relative frequencies (or preferably cover) of *Andropogon scoparius* and *Bouteloua curtipendula.* I think the Glade's general aspect and its severe selection against trees, shrubs, and woodland herbs, particularly as evidenced by selection against all but very *Ashei*-like junipers, support the conclusions of Erickson, Brenner, and Wraight (1942) that these glades are edaphic sub-climaxes.

The frequency data show the Old Field to be fairly typical for the Ozarks. There are several abundant species, but none of these contribute decisively to the field's aspect or cover. *Poa pratensis, Andropogon virginicus, Panicum virgatum, Triodia flava,* and *Rubus flagellaris* are conspicuous. While the number of species is much the same for the two areas, the Old Field has fewer species with high frequencies or very low frequencies, and more with average frequencies. The Old Field is obviously in a rapid stage of succession toward woodland.

Several other species were not found in the quadrats sampled. Mostly, these are not common plants in these areas but in some cases may occur with frequencies of 5 or 10 per cent in localized areas of the Glade or Old Field. The following species occurred on the Glade but did not occur in the quadrats: *Ulmus rubra, Celtis occidentalis, Physocarpus opulifolius, Amelanchier arborea, Rosa carolina, Prunus serotina, Rhus glabra, R. aromatica, Ilex decidua, Celastrus scandens, Acer saccharum, Cornus Drummondi, Diospyros virginiana* var. *pubescens, Fraxinus quadrangulata, Viburnum rufidulum, Sporobolus heterolepis, Elymus virginicus* forma *hirsutiglumis, Allium stellatum, Menispermum canadense, Psoralea psoralioides* var. *eglandulosa, Linum sulcatum, Petalostemum purpureum, Croton monanthogynus, C. capitatus, Asclepias tuberosa* ssp. *interior, Triosteum perfoliatum, Vernonia crinita, Kuhnia eupatorioides* var. *corymbulosa, Hypericum perforatum, Amsonia illustris, Isanthus brachiatus, Ruellia humilis, Solidago rugosa* var. *aspera, S. rugosa* var. *celtidifolia, S. nemoralis,* and *Parthenium hispidum.* A total of 80 species of vascular plants was collected on the Glade (45 from the quadrats; 35 by systematic search). Eighteen other species, mostly seedlings of the woody species already mentioned, were found in the Old Field but not in the quadrats. According to experience and estimates, it seems likely that slightly over 100 species may be found in similar areas the size of the Glade and Old Field. Since these studies did not run continuously through the seasons involved, a considerable number of species was probably missed. It is also obvious from the data that a sampling area 0.5 per cent of the total is too small for best results; an area between 1 and 2 per cent would have been effective.

The closed glade is a tension zone between the open glade and the oak-hickory woodland. It is a mixture of the open glade and oak-hickory woodland floras, but most of the cover in the arborescent layer is from juniper and chestnut oak. The transition from one community to the other seems abrupt since it occurs over a short distance, usually from 50 to 100 feet. From transect studies in the closed glade I listed 75 species, 39 of which were frequent species in the oak-hickory woodland and 43 were frequent in the open glade (Glade).

Plate 20 shows the aspect of the Glade with close-ups of two quadrats (1 meter in size) on the up-slope and two on the down-slope. Plate 21 shows the Old Field aspect with two quadrats up-slope and two down-slope.

## DISTRIBUTION OF JUNIPER SEEDLINGS

The diagonals and sides of the Old Field and the Glade were used as transects for seedling counts. All juniper seedlings were counted within one-half meter on either side of the diagonals and one meter to the inside of the area boundaries. Seedlings were divided into three classes as follows: Class 1, 18 inches or less; Class 2, 18.1–36 inches; Class 3, 36.1–72 inches. Total number of seedlings reported is based on counts in approximately one twentieth of the total area.

In the Old Field, a total of 621 seedlings was estimated, of which 276 were in Class 1, 207 in Class 2, 138 in Class 3. The actual number is probably somewhat higher since the smaller seedlings are rather easily overlooked. The seedlings were not distributed at random, but were either clumped about the mature (fruiting) female trees (with over 90 per cent of them on the down-slope side), or were more or less aggregated at the bottom of the slopes or in other areas where materials carried by run-off water are deposited. Birds play an important role in the distribution of seedlings in the Old Field. Many young seedlings were clustered below the branches of shrubs and trees other than junipers. A very few were found on isolated knolls and in the open where they may have been deposited by birds in flight or by ground-feeding birds.

The Glade supported a great many more seedlings under four years of age than did the Old Field. The estimate was: Class 1, 6,672; Class 2, 10; Class 3, 12. The total estimate was 6,764 seedlings for the 60,000 square feet of glade exclosure. These were distributed much as in the Old Field, but even more uniformly because of the greater uniformity of the 10° slope characterizing the Glade. The seedlings were either clumped on the down-slope side of the mature (fruiting) female trees or were aggregated at the bottom of the Glade slope where the *Sporobolus neglectus*, because of its increasing cover toward the lower edge, acted as a brake to tumbling berry-cones carried by run-off water. There were numerous seedlings in the open, probably from seeds deposited by birds. Great flocks of robins and cedar waxwings are a common sight on the glades, particularly in the fall after the crop of berry-cones has ripened. Fortuitous fluctuations in climate probably add to the seedling mortality. In very wet seasons the seedlings with more genes of red cedar are probably favored only to be wiped out in a later year by drought. Likewise, seedlings possessing a strong *J. Ashei* component are favored in drought seasons but may suffer defeat in wetter periods.

## POPULATION STRUCTURE OF JUNIPERUS

The variations in the junipers *(Juniperus virginiana)* of the Glade, Old Field, and Cedar Hill were studied, and five morphological characters were measured and plotted as pictorialized scatter diagrams. Two of the five characters, measured, gland length-width ratio and lateral whip length, were used on the ordinate and abscissa of logarithmic paper ($1 \times 1$ cycle) and the other three as rays on the scatter diagrams. The data for the three characters plotted as rays were grouped as follows: (1) whip-leaf length: long-bar = 8 mm. or more, half-bar = 5–7 mm., no bar = 2–4 mm.; (2) per cent decussate: long-bar = 25–100 per cent, half-bar = 6–24 per cent, no bar = 0–5 per cent; (3) terminal whip length: long-bar = 80 mm. or more, half-bar = 31–79 mm., no bar = 0–30 mm. The scatter diagrams for the Glade, Cedar Hill, and the Old Field populations, as well as for populations typical for the species, are shown in fig. 1.

Population means and ranges were obtained from the grouped data (pictorialized scatter diagrams) in the manner described in an earlier paper (Hall, 1952, p. 53). The numbers given have no absolute value but represent a graded scale or index of characteristics. The scale is made up in such a way that low scores belong to *J. Ashei*, high scores to *J. virginiana*, and intermediate scores to morphological intermediates or introgressants of the two species. From these scatter diagrams the following population means on this arbitrary scale were obtained: Glade—4.35; Cedar Hill—5.48; Old Field—10.0. Typical *J. Ashei* has a population mean of 2.0–2.3; typical *J. virginiana*, Eastern race, has a mean of 9.0–10.0.

The two characters plotted on the abscissa and the ordinate for the pictorialized scatter diagrams were also analyzed by using ordered values. The data were expected to fit a log-normal distribution which was confirmed, for the data produced a straight-line function when the ordered values (from smallest to largest) were plotted on logarithmic probability paper. I followed the practical short-cut recommended by George W. Thomson of the Ethyl Corporation, which used the range as a measure of dispersion instead of the standard deviation. Statistical techniques using the range are particularly efficient with small samples.

This is an excellent method of checking the confidence of data where only an average and the range are available. The confidence limits a, b $= \overline{x} \pm ts/\sqrt{n}$,

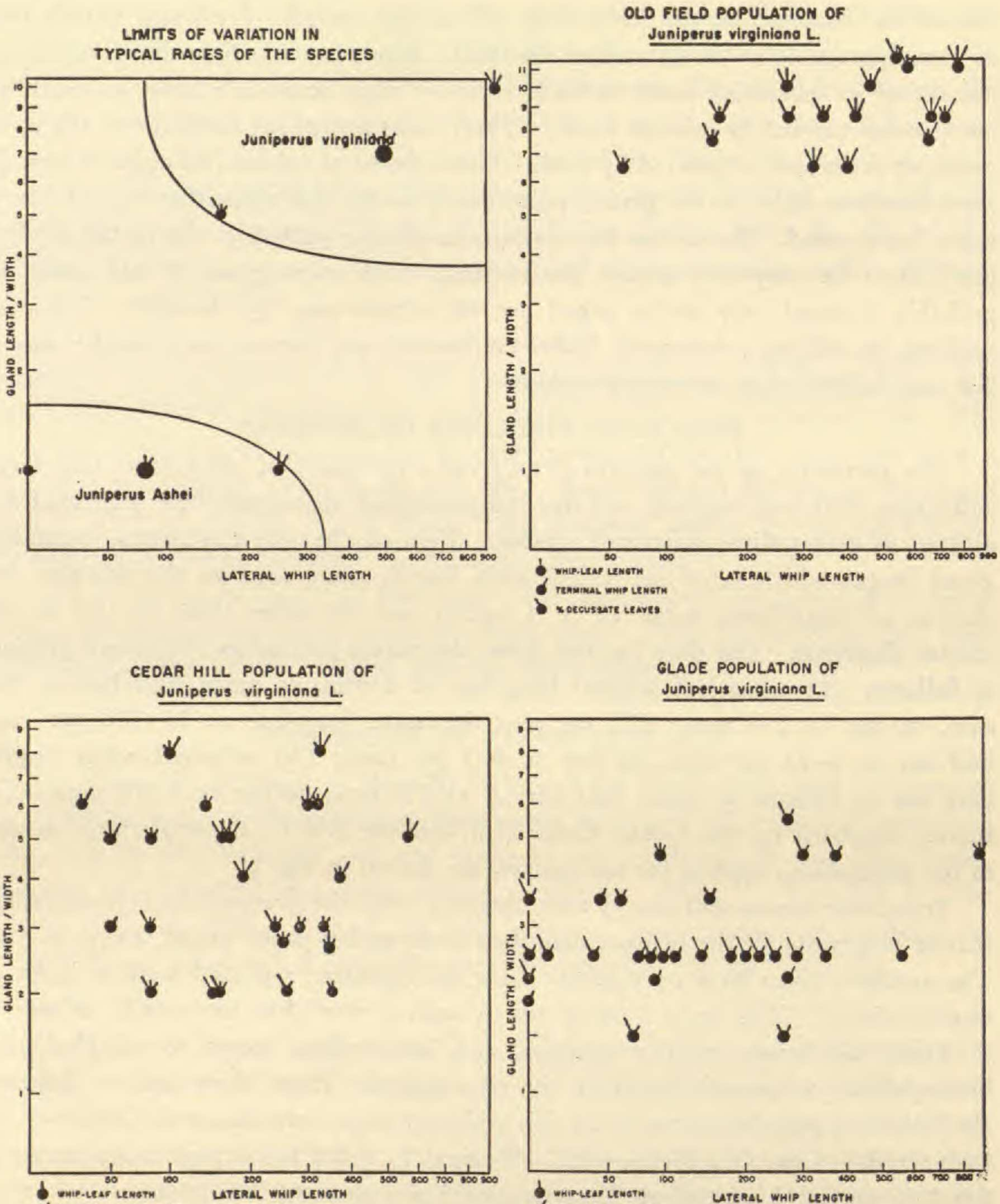


Fig. 1. Scatter diagrams showing the variations in five characters of a typical race of *Juniperus virginiana* from southwestern Virginia, a typical race of *J. Ashei* from the Edwards Plateau of Texas, and of three populations of *J. virginiana* at Gray Summit, Mo. The diagram at the upper left for the typical races shows the means (large dots), the extremes (small dots), the limits of variation (the curved lines). (The symbol in the space at the upper right of this diagram should have had three long arms.) In the diagrams for the three Gray Summit populations each dot represents a single individual.

where $\bar{x}$ is the mean, t is Student's t, s is the square root of the estimated population variance, and n is the number in the sample. Or, by using the short-cut the 95 per cent confidence limits are equal to the range multiplied by the proper value[1] (0.1064 for n = 25, 0.0720 for n = 42) plus or minus the mean.

Table II lists the population means, confidence limits, and standard deviations (log values) for two characters of each of the three populations and typical populations of both *J. Ashei* and *J. virginiana.* Figure 2 represents the ordered values plotted on logarithmic probability paper. The slopes of the lines depend on the amount of variation within each group; the greater slopes indicate the more heterogeneous populations. The point of intersection of each line with the 50 per cent value is the estimated mean for each population. The points of intersection of the 25 per cent and 75 per cent values with each line delimit the range where half the values for that character will probably lie. In fig. 3 rectangles are made about the means to correspond to the 50 per cent probability level, and the farther two rectangles are separated the greater the probability that the difference between the corresponding means is not due to chance. The dotted lines indicate the 95 per cent confidence limits of the means from Table II.

These five populations were compared to determine the probability that they represent the same population with equal means by means of the t-test. If one assumes the means of two populations to be equal, the sample difference is tested to see whether it is no more than sampling variation from the hypothetical difference, zero. Each of these comparisons led to a large t value, indicating a low probability that they represent samples from a single population. Welch's modification of the t-test was used for the comparison because the variances were not homogeneous (Comparison of $\mu_1 - \mu_2$ regardless of $\sigma_1^2/\sigma_2^2$).

TABLE II

MEANS AND THEIR 95 PER CENT CONFIDENCE LIMITS FOR TWO CHARACTERS IN FIVE POPULATIONS OF *JUNIPERUS*

| Populations | Age Class | Number in sample | Whip leaf length (mm.) | | | Gland length/width | | |
|---|---|---|---|---|---|---|---|---|
| | | | Means | Conf. limits | Stand.* dev. | Means | Conf. limits | Stand.* dev. |
| *J. Ashei* | 30 yrs. | 25 | 4.8 | (4.0–5.7) | 0.179 | 1.0 | (0.95–1.05) | 0.045 |
| Glade | 35 yrs. | 42 | 2.6 | (2.3–3.0) | 0.500 | 2.2 | (2.0–2.5) | 0.145 |
| Cedar Hill | 30 yrs. | 25 | 6.8 | (5.9–8.0) | 0.522 | 3.9 | (3.4–4.5) | 0.187 |
| Old Field | 20 yrs. | 25 | 7.2 | (6.3–8.3) | 0.140 | 8.1 | (7.6–8.8) | 0.093 |
| *J. virginiana* | 30 yrs. | 25 | 8.8 | (8.1–9.6) | 0.088 | 6.4 | (6.0–6.9) | 0.100 |

* Log values.

[1] See the Appendix to this paper. The values for these multiplying factors were worked out for sample numbers from 2 to 1000 by George Thomson and appear in Table III.

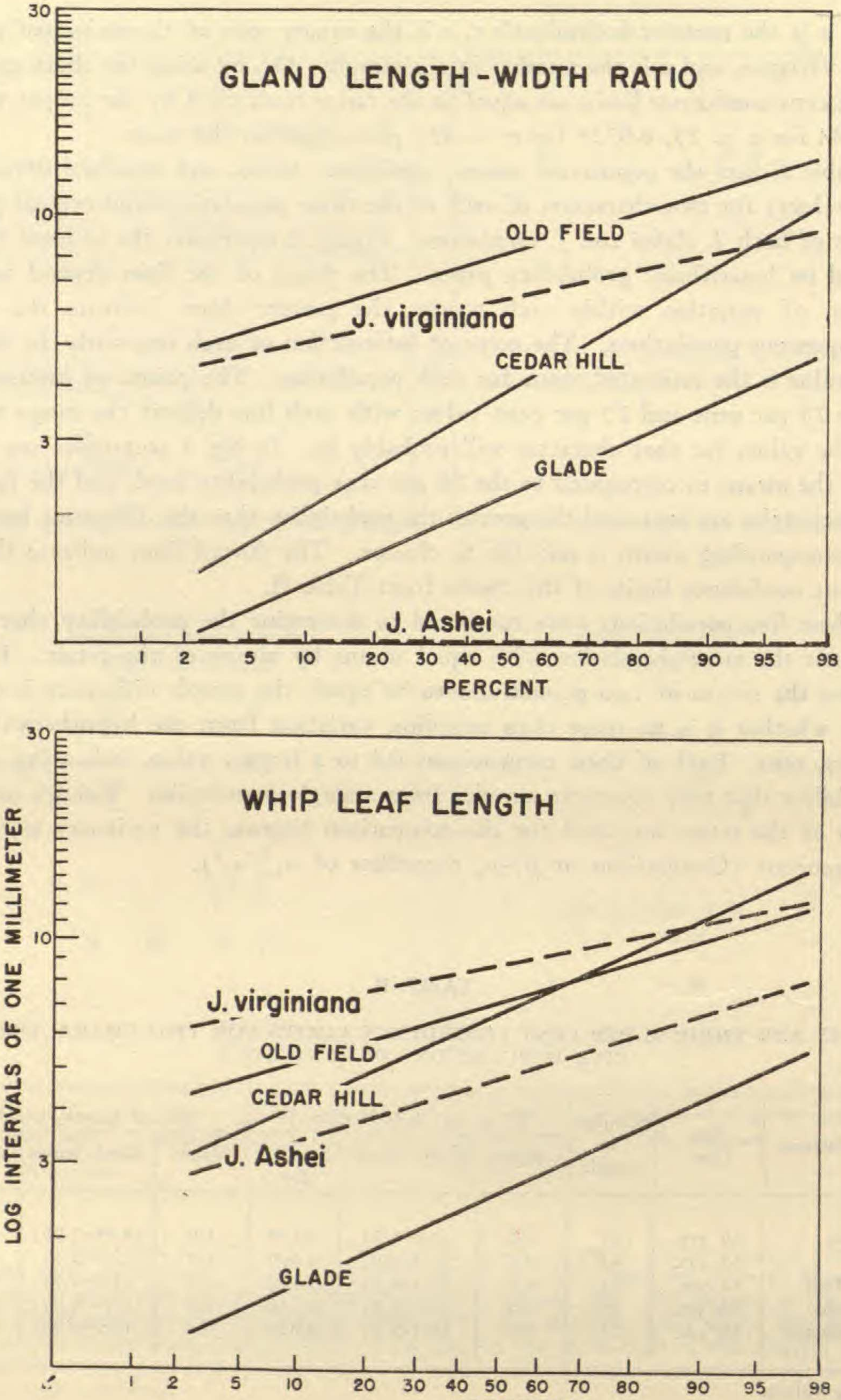


Fig. 2. Ordered values, plotted on logarithmic probability paper, for two characters for typical populations of *Juniperus virginiana, J. Ashei,* and the three populations of *J. virginiana* from Gray Summit. Length of the lines delimit the range where 95 per cent of the values for these two characters will probably lie.

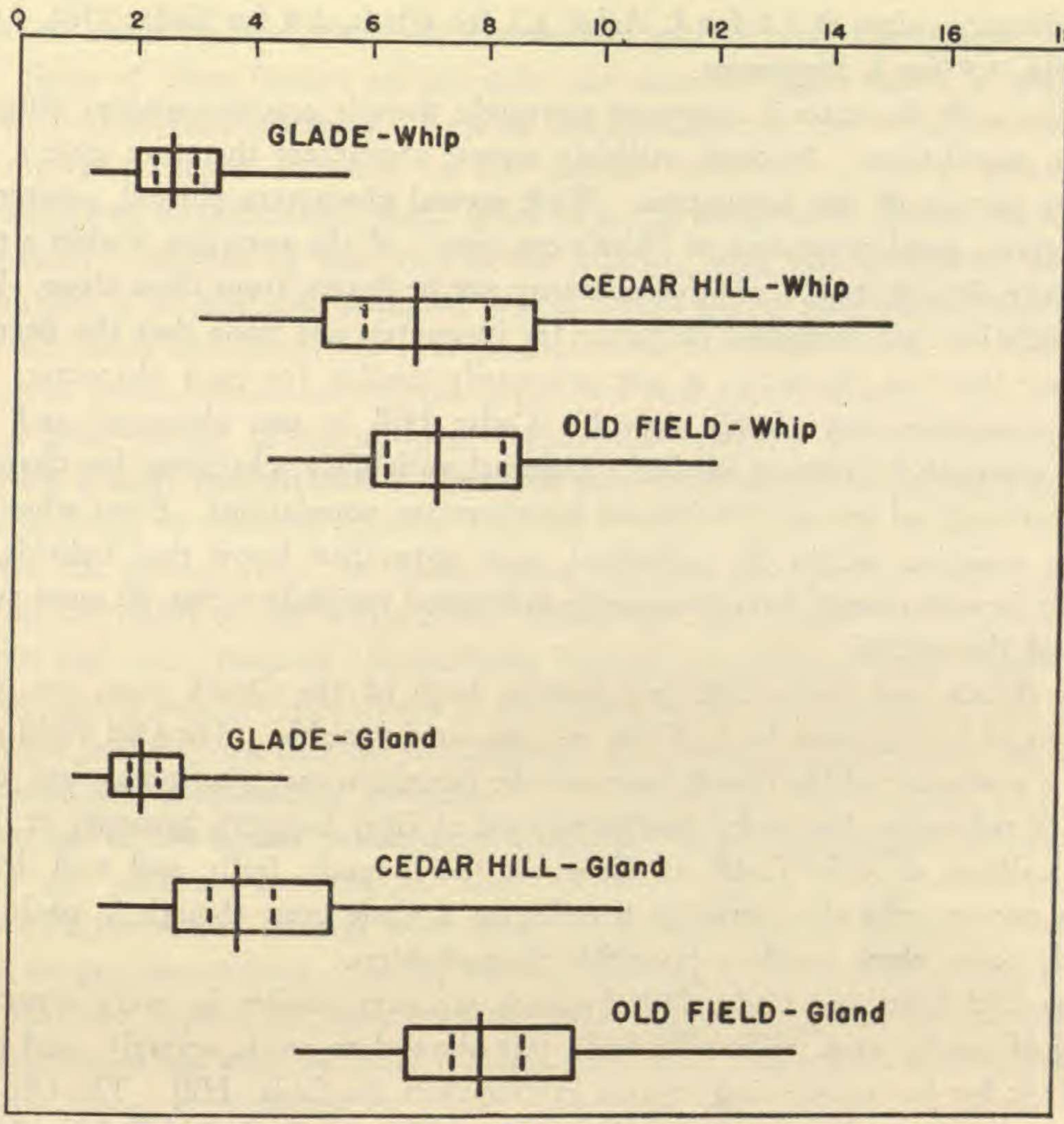


Fig. 3. Variation in whip leaf length and gland length-width ratio in the three populations of *Juniperus virginiana* from Gray Summit, Mo. The estimated means are represented by vertical bars; the 95 per cent confidence limits of the means by vertical dashes; the rectangles delimit the ranges where 50 per cent of the values will probably lie; the length of the horizontal lines delimit the ranges where 95 per cent of the values will probably lie.

## DISCUSSION

In the Missouri Botanical Garden Arboretum at Gray Summit, Missouri, these three populations of *Juniperus virginiana* called here Glade, Cedar Hill, and Old Field, are each distinct, having considerably different variances and significantly different means. Each is also distinct from either species, *J. Ashei* or *J. virginiana*, which contribute to the variability of these Ozark populations. Yet, these three Ozark populations exist within less than a mile of one another, but in habitats which, at least in part, may be noted for their differences more than their similarities. In the sums of several morphological characters these populations differ from one another in nearly the same degree, so that a crude ranking using five characters gives arbitrary values of 1.0 for *J. Ashei*, 2.1 for Glade, 3.0 for Cedar Hill, 4.0 for Old Field, 4.9 for *J. virginiana*.

Where each character is compared separately there is greater apparent difference between populations. Methods utilizing several characters therefore give a more accurate picture of the population. With several characters plotted, scatter diagrams give a good impression or "bird's eye view" of the variation within a population even though statistical inferences may not be drawn from them alone. When the populations are compared character for character, one finds that the degree of difference between characters is not necessarily similar for each character. The Glade population may closely resemble Cedar Hill in one character and more closely approach *J. Ashei* in another. Unequal variability, character for character, is characteristic of species hybrids and introgressant populations. Even when considering variation within the individual, most naturalists know that hybrids, particularly in wide crosses, have more intra-individual variability than do more typical plants of the species.

The Glade and Cedar Hill populations, both of the Ozark race, i. e. introgressants of *J. virginiana* by *J. Ashei*, are the most variable. The Old Field population is a mixture of the Ozark race and the Northern race (including var. *crebra* type) of red cedar; but as far southwestward as Gray Summit, Missouri, it occurs sporadically in disturbed habitats where the soil is sandy, light, and well drained. I have not yet seen this northern invader on a glade even though it could conceivably occur there within a favorable micro-habitat.

The Old Field and Cedar Hill habitats are very similar in every aspect but history of use by man. The Old Field was allowed to erode severely, and consequently it has less topsoil and organic matter than the Cedar Hill. The Old Field soil is more acid, sandy and coarser than Cedar Hill soil. Both Old Field and Cedar Hill soils are quite different from the very thin, organically rich, spring-wet, summer-dry soil of the Glade.

The Northern race of red cedar (including var. *crebra*) tends to be arenicolous, and even though it develops well on sandy areas overlying limestone or on the strands of marly lakes, it does best on slightly acid, well-drained strand or dune areas where competition with other plants is at a minimum. The Northern race becomes more arenicolous as it becomes more columnar or spire-like. Because of the ease with which junipers may be distributed over great distances, it is not surprising to find an occasional mixture of the Northern race of red cedar in the northeastern Ozarks. However, its occurrence there is a result of man inadvertently preparing a suitable habitat, an eroded, acidic, sandy field with poor cover. Except for the minor role the Northern race plays in introgression with the Ozark race, its effect on the Ozark populations is transient and dependent on the perpetuation of poor land-use practices. Ozark fields which have had fair treatment, particularly where cover has been protected, support stands of the Ozark race alone. In part, the Ozark race is also dependent on man since a large number of its populations occur on cleared or grazed land.

Several other factors affect the distribution and structure of juniper populations. Some of these factors are intrinsic and some extrinsic, but it is impossible to consider them independently. Rate of reproduction, per cent viability, presence of introgressive genes, character of the climatic extremes (whether unfavorable for natural seed stratification, which seems to be the situation at the northern limits of red cedar), amount of bare area in the habitat, slope, soil conditions, presence and abundance of bird and mammal species which aid in seed dissemination, role of run-off water and gravity in seed dissemination, and several other factors occur in different combinations and degrees to produce populations ranging from uniform (as in a cedar-brake) to less uniform (apparently random) to clumped. In general, when a large enough area is examined there may be found "parent" populations consisting of cores of ancient specimens which supply or supplied the seed stock for the general area. In southwestern Missouri these mother-plants may be found on the bluffs of the White River where they have fruited for centuries safe from fire and other hazards. In northern Missouri the bluffs of the Missouri and Meramec Rivers support populations of ancients. These bluff habitats of the major rivers were probably the original environment for *Juniperus* long before the Ozark glades were first colonized by junipers.

On most of the glades in the eastern Ozarks the oldest junipers are over 100 years of age, probably between 125 and 135 years. Since all the older junipers from which increment borings were taken were hollow at the center, it was not possible to get precise ring counts, but by applying a factor determined by the rate of decrease in years per inch from the center to the outside of an increment, a good estimate of age may be made. Much older trees (judged by circumference) have been found occasionally on bluffs throughout the Ozarks, but those from which increments were taken were hollow and usually with more or less eccentric rings. Such old junipers are not found in Ozark fields. In the early years of the 19th century and previously, written accounts of travels and casual reports by geologists indicate that junipers were to be found only along bluffs of the major rivers, but reports in the last half of that century presented a picture of juniper distribution much as it is today. Wherever the rocky limestone glades are burned each year, they are devoid of junipers and shrubs, giving an open grassland aspect with an abrupt transition to forest at the edges. Also, the junipers do not easily invade a glade that has been protected from grazing and supports a good stand of grass. The treeless glades, which are not uncommon, always have good cover and protection from man's grazing animals. Where glades show signs of erosion junipers are localized. In general, juniper density is proportional to the degree of land abuse, so that glades may support junipers distributed as dense "brakes", open stands with evenly but widely spaced individuals, or scattered, clumped colonies. Because of the nature of the glades slight grazing could easily weaken the cover to permit invasion of junipers where fire-sere grassland would not be so easily weakened. Before white man came to the Ozarks, wild herds probably initiated the invasion of the glades by junipers; white man tremendously accelerated the process through his domestic animals.

In an earlier paper (Hall, 1952) I suggested that introgression between *J. Ashei* and *J. virginiana* may have begun as early as the late glacial period, followed by an expansion during the xerothermic period. Throughout this time, before settlement of the Ozarks, the most continuous habitats for junipers were the bluffs, knobs, rough glades, and youthful streams or rivers with flood-plains in an early stage of succession. Probably continuously the bluffs, knobs, and glades (edaphic subclimaxes) were inhabited by *Ashei*-like junipers while the streams and river banks supported scattered stands of *virginiana*-like plants.

The distribution pattern of junipers in the Ozarks has probably changed radically since settlement. It is clear that the oldest junipers are situated on bluffs or glades, while old fields in the St. Louis area may support mature colonies (oldest plants up to 70 years) of the Ozark race or occasionally more youthful colonies (40 years or less) of the Northern race mixed with Ozark. From this study and cursory examination of other fields, it is evident that the condition of the land in large part determines the kind of junipers selected from the local gene pool. Literally, explosive distribution of juniper has occurred in the last hundred years, progressively increasing in amplitude as abused or worn-out land was abandoned to old-field succession. The fact that these neighbor populations, particularly Glade and Old Field, are distinct even though intermediate does not mean that hybridization between them is limited, but that each habitat is selecting the best-adapted genotypes. Natural selection is strong enough to limit the portion of the available gene pool which may be realized. Here are two powerful forces working against one another. Strong natural selection restricts the gene pool; hybridization amplifies it. With species like those of *Juniperus*, which hybridize freely and are readily dispersed, I suggest that continuously variable habitats result in continuously variable populations, and the simplest situation is when the hybridization is between two allopatric species.

Anderson (1948) stated that hybrids between two species differing in habitat requirements are expected to occupy intermediate habitats. The $F_1$ should occupy a habitat more or less intermediate between the two species; the $F_2$ should occupy more variable habitats, but the range should lie between the habitats of the species; backcrosses or introgressants should occupy habitats closest to the backcross parent. Two species may be quite interfertile, exist side by side, yet show little evidence of hybridization between them because the habitats select the parent-type combinations. If the habitat is disturbed, these available mongrels may become established. The homes of these variants are the seres either initiated by natural processes or man. While hybrid swarms and hybrid habitats are transient, they have their influence toward increasing variability both through cryptic processes, e. g. structural differentiation, and toward accelerating regional differentiation. If, for the sake of discussion, man as a producer of hybrid habitats is ignored, it will be seen that processes which initiate succession produce hybrid habitats, and indeed the edges of ecologic systems, physiographic provinces, and climatic regions are hybrid habitats. Ecologic tension zones are hybrid habitats where species which meet may develop discordant variability. When man enters the scene, the pattern becomes more complex. Hybridization may do its cryptic work in tension zones through all levels of ecologic structure. The obvious evidence of hybridization, the hybrid swarms, are transient; and they may occur whenever the right hybrid habitat is available, but in most situations the habitats select gene combinations more like the parents and tend to keep the populations distinct.

SUMMARY

In the northeastern Ozarks *Juniperus virginiana* is represented by the Ozark race (introgressants from *J. Ashei*) on bluffs, glades, and most old fields. Occasionally, the Northern race is found locally with a little admixture of the Ozark race. Three populations of *J. virginiana* in the northeastern Ozarks were studied in detail in order to compare their variation patterns and habitats. Variation patterns were compared by means of scatter diagrams for five characters and ordered values, means, 95 per cent confidence limits, and standard deviations for two characters. The t-test modified by Welch was used to compare the means of the populations. Habitats were compared in terms of their histories, slope, soil profile, flora, frequency of species, rough estimates of cover, seedling distribution.

The evidence suggests that the three populations—Glade, Cedar Hill, and Old Field—are distinct and differ more or less proportionately to the differences in their habitats. The Glade (Ozark race) is the most southwestern in affinity, more closely resembling a population and habitat of *J. Ashei.* Cedar Hill (Ozark race) is intermediate between Glade and typical red cedar and occurs on old fields which are in good condition or, farther southwestward from Gray Summit, Missouri, on more worn-out lands. The Old Field (Northern race with a little mixing from the Ozark race) occurs on worn-out acidic and sandy lands in the vicinity of St. Louis and northeastward.

Extremely high seedling mortality (much higher on the Glade than Old Field) suggests that strong natural selection restricts the field for variability even in the face of considerable hybridization. The present balance between these two evolutionary forces depends on man making and keeping available a variety of suitable habitats. A shift in habitat qualities will result in a shift in the variation pattern of the junipers.

Distribution of age classes in the junipers indicates that the bluffs, knobs, and glades have been colonized longest by junipers, followed by the old fields supporting the Ozark race, and last the worn-out sandy, acidic fields supporting youthful colonies of the Northern race. An explosive expansion of juniper colonization resulting from man's activities seems to have occurred within the last hundred years, growing progressively as land has been worn out and abandoned. It is proposed that man is primarily responsible for the present explosive evolution in *Juniperus* in eastern North America and that if his influence were removed from

the scene, the field of variability would decline as the area of occupation contracts. Without man's help junipers would be more or less restricted to the areas in a natural state of arrested development such as the bluffs, knobs, and glades.

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## Explanation of Plate

### PLATE 20

Aspect of Glade

Fig. 1. Open glade looking south.
Fig. 2. Open glade looking north.
Figs. 3 and 4. Two quadrats in open-glade up-slope.
Figs. 5 and 6. Two quadrats in open-glade down-slope.

1

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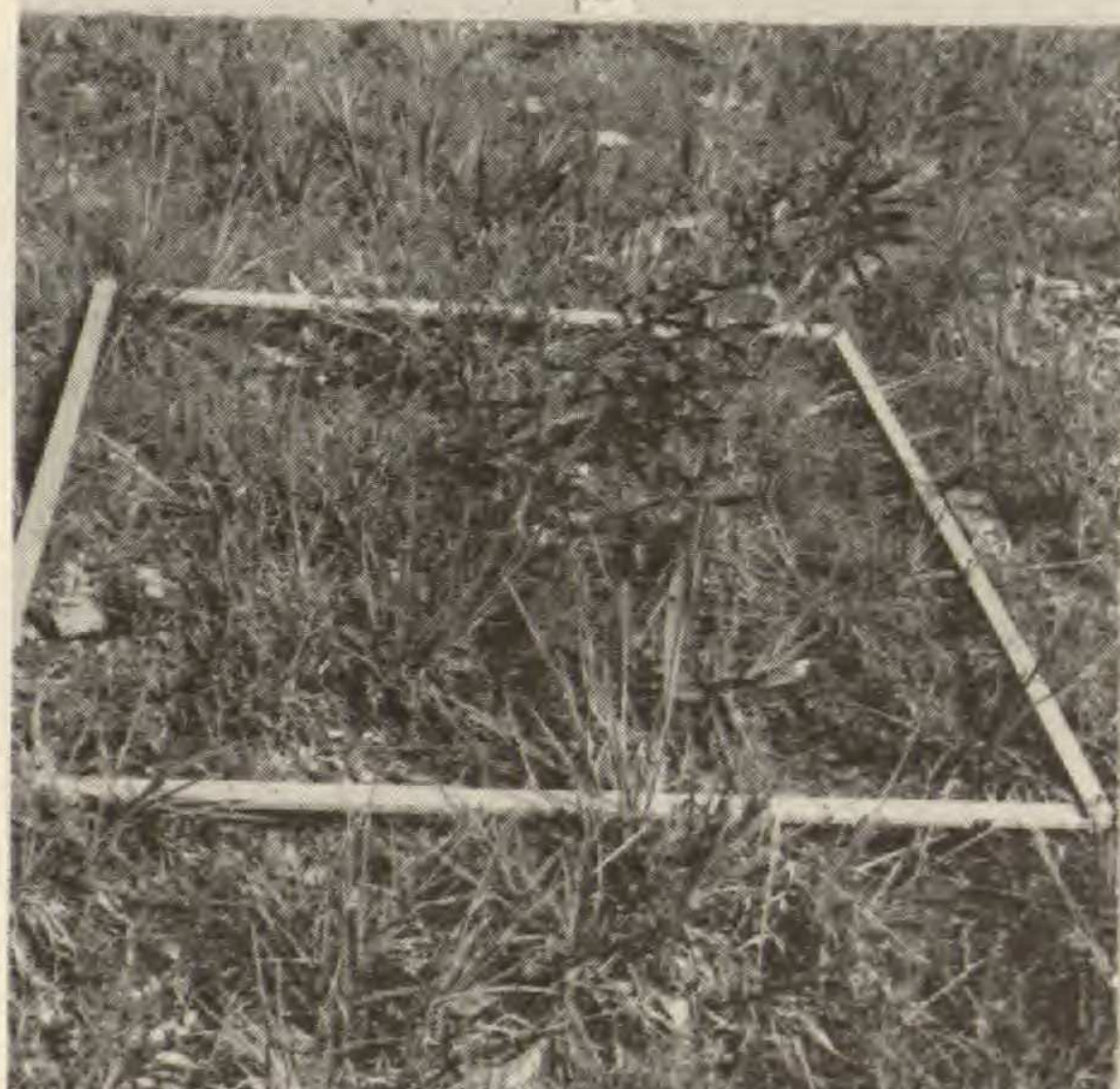

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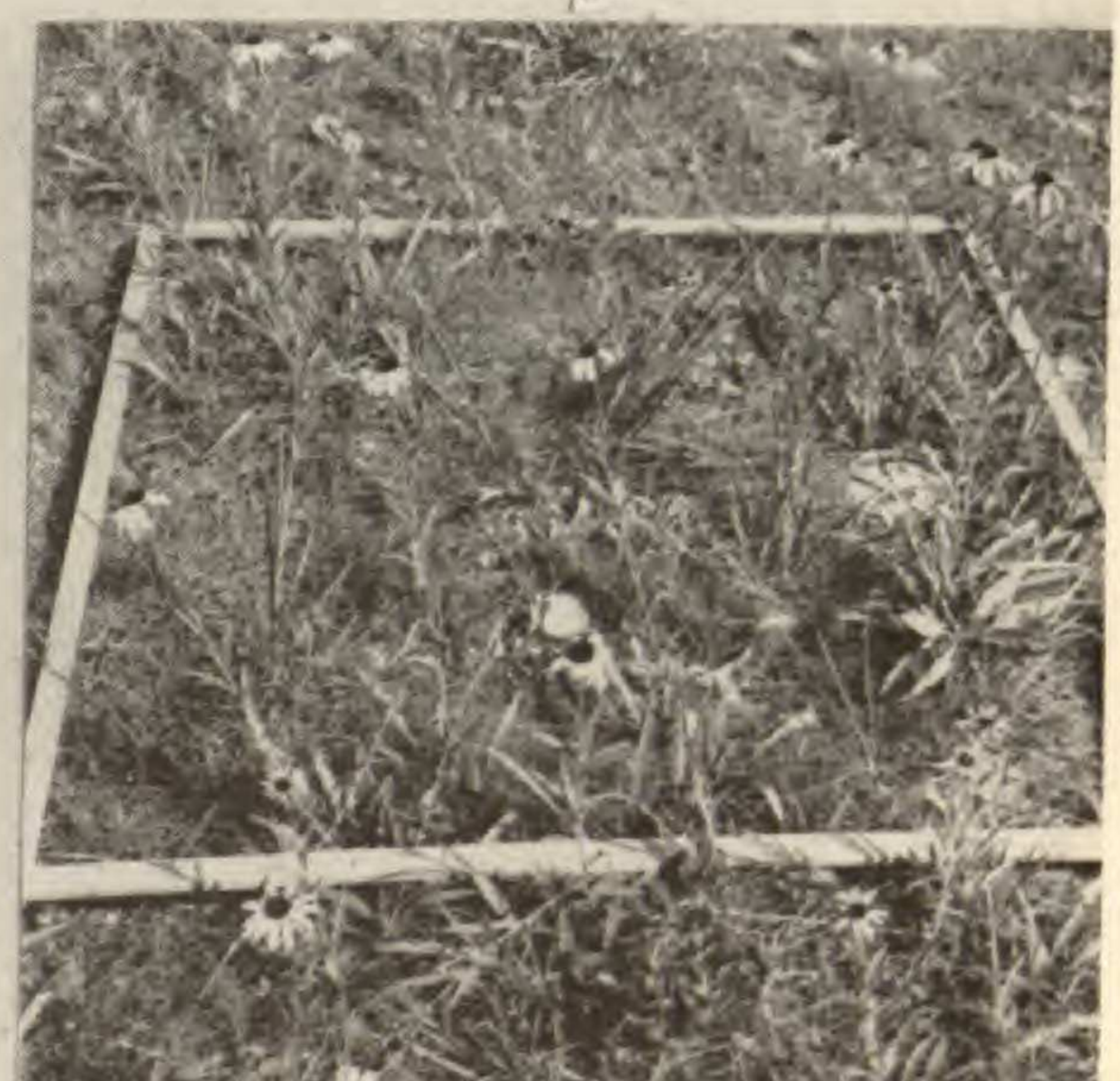

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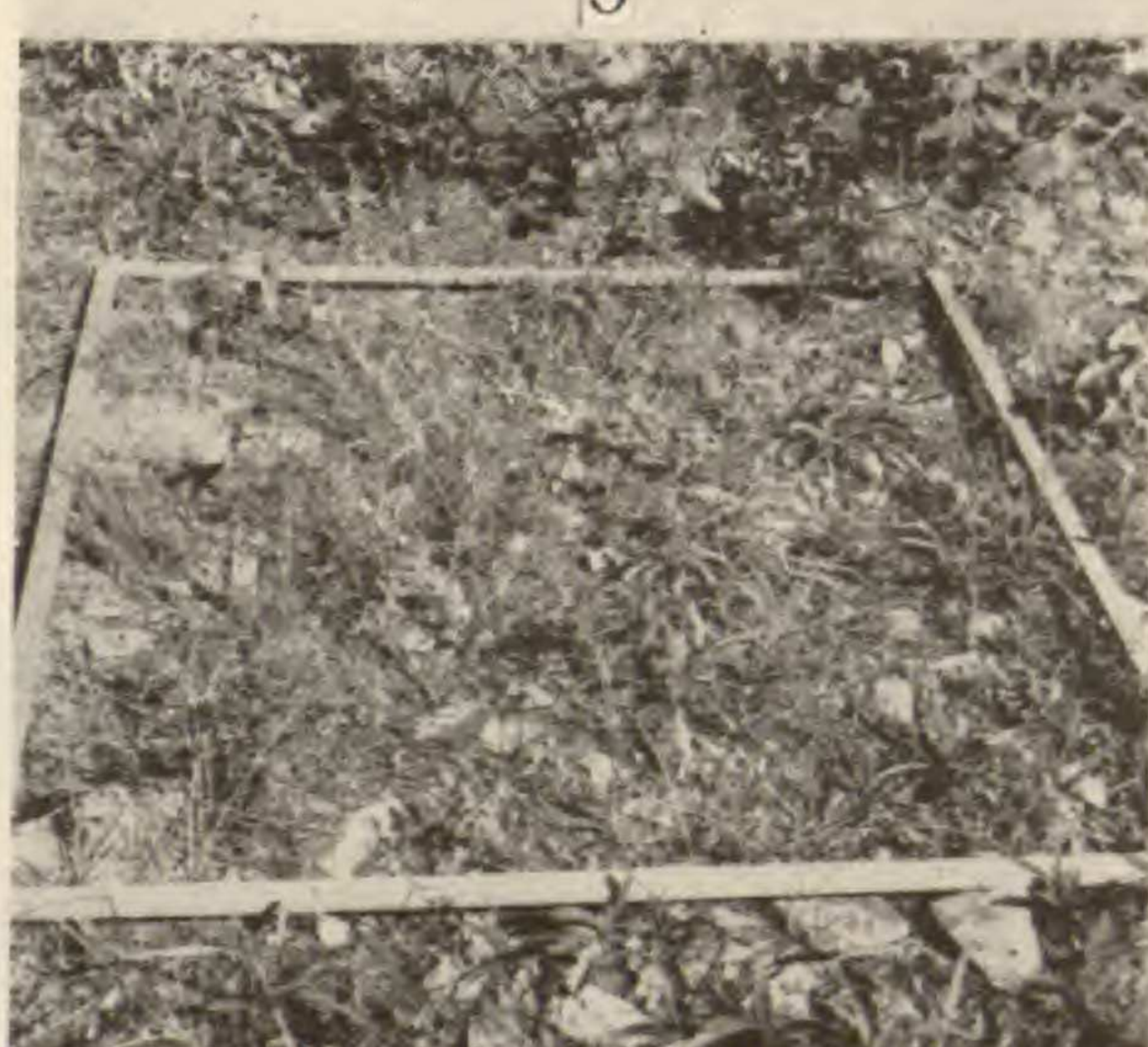

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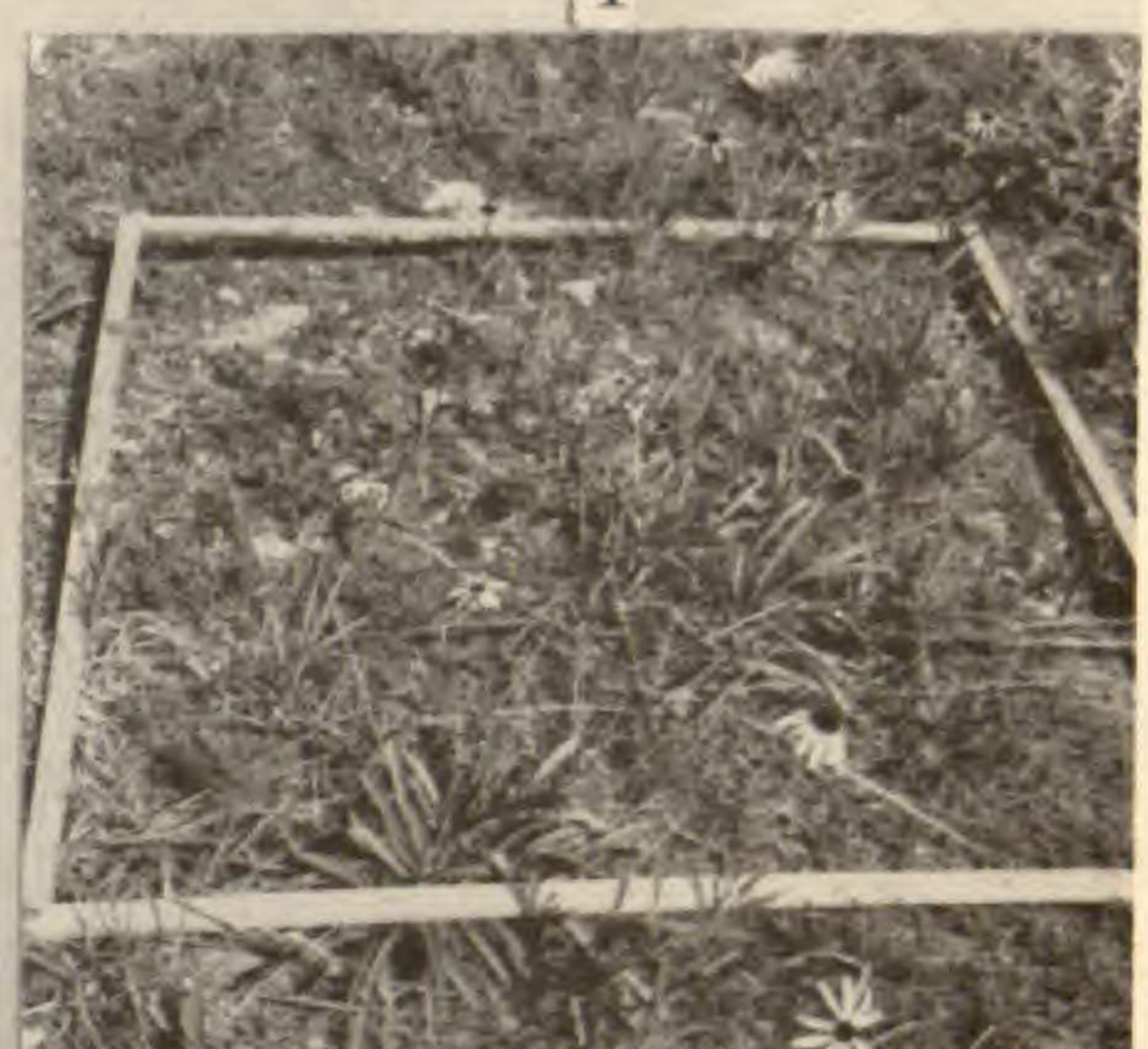
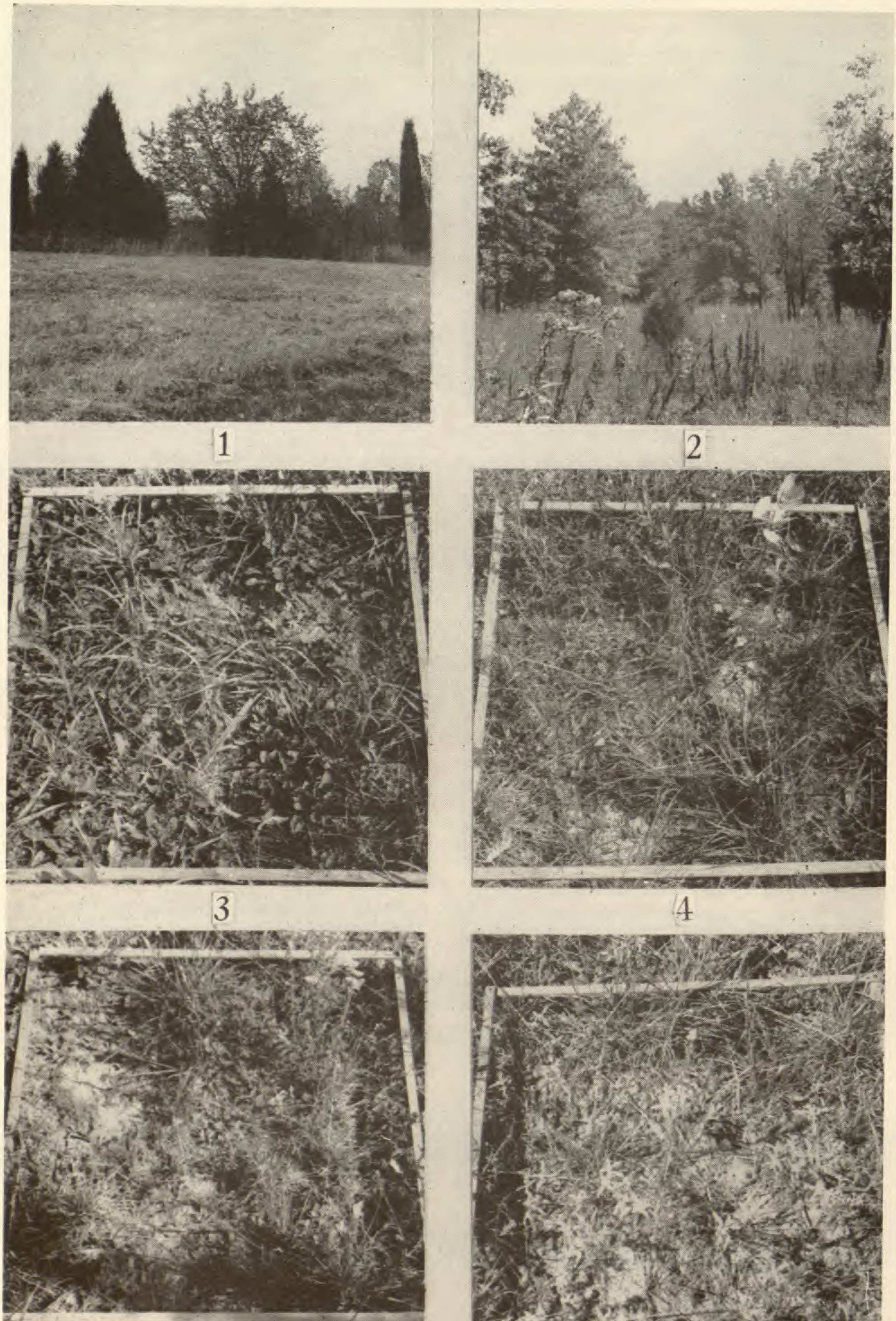


6

HALL—OZARK JUNIPER POPULATIONS




HALL—OZARK JUNIPER POPULATIONS

## Explanation of Plate

PLATE 21

Aspect of Old Field

Fig. 1. Old Field begins beyond mowed area.
Fig. 2. Old Field, interior.
Figs. 3 and 4. Two quadrats, up-slope.
Figs. 5 and 6. Two quadrats, down-slope.

## APPENDIX

### ESTIMATION OF CONFIDENCE LIMITS OF POPULATION MEAN FROM RANGE

I am very grateful to George W. Thomson for the method by which 95 per cent confidence limits of the mean may be rapidly estimated by multiplying the sample range by a factor. Lord (1947) prepared a table of factors for sample sizes from two to twenty for six classes of probability (90–99.9 per cent). Thomson prepared a table of factors including greater sample sizes for 95 per cent probability. Thomson's table and brief discussion are published here for the benefit of other biologists who may wish to use this short method of getting 95 per cent confidence limits of the mean.

The usual method of estimating the variability of a population from a sample is by the use of the usual standard deviation estimator, s. However, recent research has shown that much more convenient estimates can be obtained from the sample range, which is defined to be the difference between the smallest and the largest values in the sample. These estimates are not as efficient in the statistical sense, but the loss is not important from a practical point of view. A useful by-product of this research is the rapid estimation of confidence limits of the mean of a normal population by the multiplication of the sample range by a factor. These results are associated with a smaller number of equivalent degrees of freedom than confidence limits based on the usual s estimates of the population standard deviation. A close approximation for the multiplying factors was found by Patnaik (1950) who approximated the distribution of the range in normal samples by the $\chi$— distribution.

If w is the range in a sample of size n, then $w/\sigma = c\ \chi/\sqrt{\nu}$ where c is a scale factor and $\nu$ is an equivalent number of degrees of freedom for $\chi$.

The following table extends previous calculations (Thomson, 1953) to sample sizes as large as 1000.

TABLE III
SCALE FACTORS AND EQUIVALENT DEGREES OF FREEDOM FOR X—APPROXIMATION TO RANGE IN NORMAL SAMPLES*

| Numb. in sample n | Degrees of freedom $\nu$ | Scale factor c | Equivalent two-sided 5% t | Confidence limits** $\pm t/(c\sqrt{n})$ |
|---|---|---|---|---|
| 2 | 1.0000 | 1.41421 | 12.7062 | 6.3531 |
| 3 | 1.9846 | 1.91155 | 4.3349 | 1.3093 |
| 4 | 2.9291 | 2.23887 | 3.2265 | 0.7206 |
| 5 | 3.8267 | 2.48124 | 2.8267 | .5095 |
| 6 | 4.6772 | 2.67253 | 2.6249 | .4010 |
| 7 | 5.4841 | 2.82981 | 2.5038 | .3344 |
| 8 | 6.2512 | 2.96288 | 2.4233 | .2892 |
| 9 | 6.9818 | 3.07794 | 2.3658 | .2562 |
| 10 | 7.6798 | 3.17905 | 2.3228 | .2311 |
| 11 | 8.3485 | 3.26909 | 2.2894 | 0.2112 |